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A quantitative description of shoot development in *Calamus caesius* (*Palmae : Calamoideae*)

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Summary. The morphology and growth in the apical region of 15 stems of *Calamus caesius* Bl. was studied over fifty two days in a 15-year-old plot. Morphological study showed that the apical meristem was hidden within leaf sheaths about 79 cm below the knee of the youngest expanded leaf. Growth measurements showed that the internode whose distal end bears the youngest leaf with expanded pinnae, but not the older ones, was still expanding, and was about 16% shorter than its mature length. Leaf production averaged 1 per 24 days (15.2 leaves per year). Estimated longevity of expanded leaves was about 4.1 years. These measurements provide the basis for a dynamic model of growth.

For the estimation of the yield in a rattan stand, Lee (in press) suggests several models which are based on mathematical relationships between the number of internodes and the yield parameters of interest to the rattan growers, *i.e.* the length, volume and weight of the stem. These models assume constant or gradually increasing internode length from stem base to tip. However, Fisher (1978) has shown that the last three internodes, whose distal ends bear a frond with expanded pinnae, are still elongating in *Calamus manan* Miq. and *Daemonorops angustifolia* (Griff.) Mart. This feature of rattan shoot development has implications for the practical use of the models proposed, especially in young plants. The present study thus aims to determine the extent of elongation of these developing internodes compared with the eventual length when they have fully elongated, for a widely cultivated small-diameter species, *Calamus caesius* Bl.

The temporal component of this study also permits the estimation of the rate of leaf production, an essential component of any dynamic model of rattan growth. The rate of growth over the lifetime of a stem can be estimated by counting the number of internodes, and dividing by stem age (mean annual increment). For a stem of unknown age the time between the production of successive leaves (the plastochrone) provides a means to estimate current growth rate. Therefore this study also attempts to estimate the plastochrone for this species. The longevity of the leaves of *C. caesius* may also be estimated from the number of living fronds on the stem and the plastochrone.

Materials and methods

Fifteen *C. caesius* stems from four 15-year-old clumps growing on alluvial soil in the arboretum of the Sabah Forestry Department's Forest Research Centre at Sepilok were tagged and their length to the end of the youngest visible leaf sheath was measured (Table 1). The stems chosen have crowns exposed to a rather narrow range of light intensity, *i.e.* visually estimated to be 30-50% of the open. The leaf production and

Table 1. *Calamus caesius* stems selected for investigation of immature internodes in the Arboretum of the Forest Research Centre, Sepilok.

Clump	Sex	Stem number	Stem length (m) at beginning of study
A	Male	1	23
		2	27
B	Male	3	20
		4	21
		5	21
C	Male	6	4
		7	4
		8	12
		9	21
D	Female	10	10
		11	14
		12	14
		13	16
		14	26
		15	27

the length of the four youngest internodes whose distal ends bear fronds with expanded pinnae were recorded at 48-hour intervals over 24 days from 3rd to 27th May, 1993. Thereafter observations were carried out at weekly intervals for four more weeks. As it was impossible to measure the internode length directly without removing the several layers of overlapping leaf sheath (which would have adversely affected the growth of the stems), the internode length was determined indirectly by measuring the distance between the adjacent knees (swellings at the junction between petiole and leaf sheath, Fig.1) with a ruler. Internode diameter was not measured for the same reason. New internodes were recorded only when the pinnae of the fronds at their distal end had expanded. Precautions were taken to minimize disturbance to the stems being studied. However, in order to gain access to the stems and in the process of determining their initial length, disturbance was inevitable and some of the fronds below those being studied were cut.

To determine the reliability of the indirect method of measuring internode length, two stems, nos. 8 and 9 were destructively sampled. The lengths of the last 7 exposed leaf sheaths (leaves L_1-L_7, Fig. 1) and the corresponding internodes (I_1-I_7) were measured with a tape or a ruler to determine the position of the youngest fully elongated sheath. To confirm the basipetal elongation and maturation of leaf reported by Fisher (*op. cit.*), the lengths of the cirri, and the "leaf proper" (the leaflet-bearing rachis and petiole) were similarly measured. The lengths of the internodes, leaf sheaths, "leaf proper", and cirri shorter than 0.5 mm were not measured; and the internodes and leaves which were too small to count with the naked eye were examined under a dissecting microscope.

Results

The morphology of the apical region of a *C. caesius* stem is shown in Fig. 1. In what follows, the position of the various plant parts is defined with reference to the youngest leaf with expanded pinnae (L_1 in Fig. 1). Leaves younger than this are given zero or negative subscripts, and those older, positive.

Internode development is shown in Fig. 2 for stem 1. From this graph the average plastochrone for the stem was estimated to be 20 days during the period of observation. The plastochrone for the other 14 stems was similarly estimated. For the 15 stems investigated, the mean plastochrone as determined graphically in this manner was 24 days (95% confidence interval: 22-26 days). A plot of the plastochrone against the initial stem length (Fig. 3) shows a trend of decrease in the plastochrone with stem length. However, the correlation is not significant ($r = 0.45$, $df = 14$, $p = 0.1$). An analysis of variance, with the initial stem length as the covariate, shows that the plastochrone did not differ among the four clumps investigated.

Fig. 2 also shows that in *C. caesius*, only the last internode (I_1) whose distal end bears a frond with expanded pinnae is still extending. On average, this internode is 84% (95% confidence interval: 80-88%) of the eventual length when it is fully expanded.

The ontogeny of the leaf and internode was followed by examining them along the stem from the apical meristem to the fully expanded mature leaves of the two shoots, one of

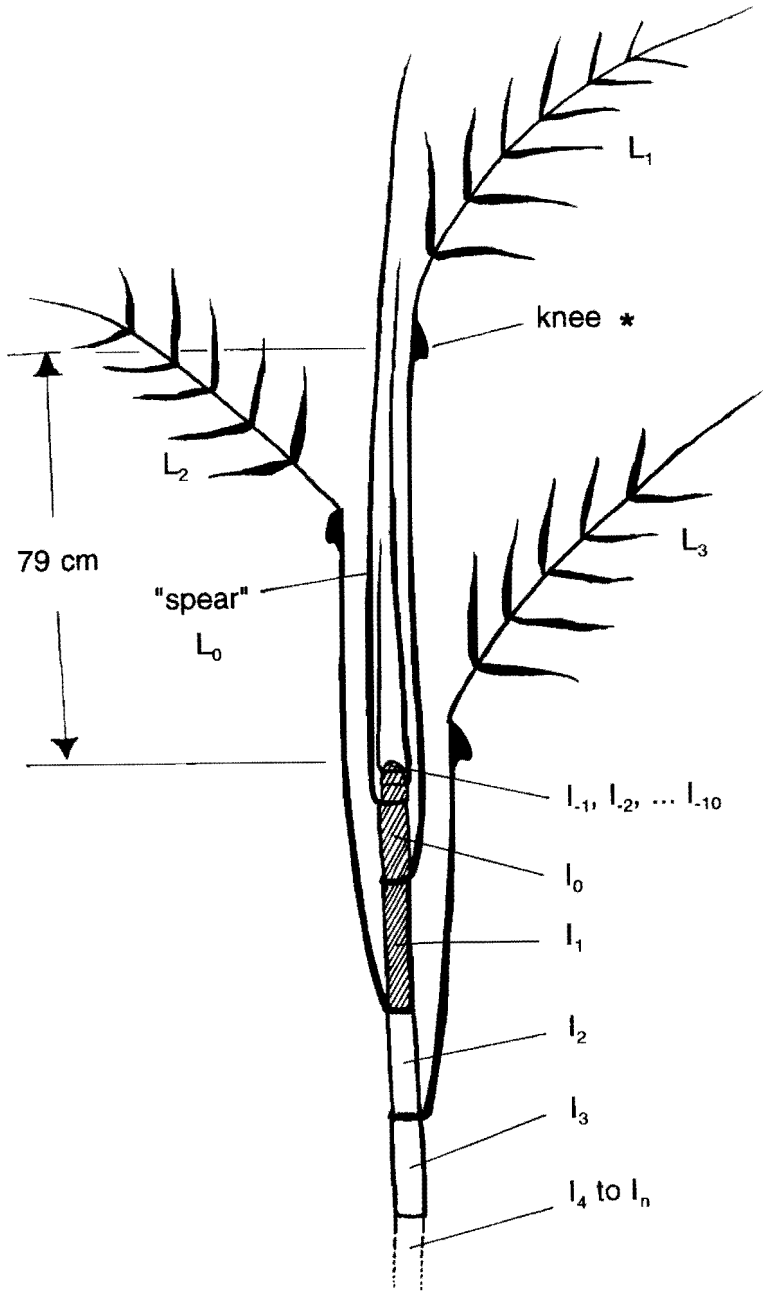

Fig 1. Diagram to show the morphology of the apical region of a *Calamus caesius* stem. Each unit comprises an internode (I), surmounted by a leaf (L), which itself is composed of a sheath (including a knee), the "leaf proper" (petiole and leaflet-bearing rachis), and a cirrus. Fully expanded internodes (I_2, I_3, I_4) are unshaded, immature internodes (I_1, I_0, I_{-1}...) are shaded.

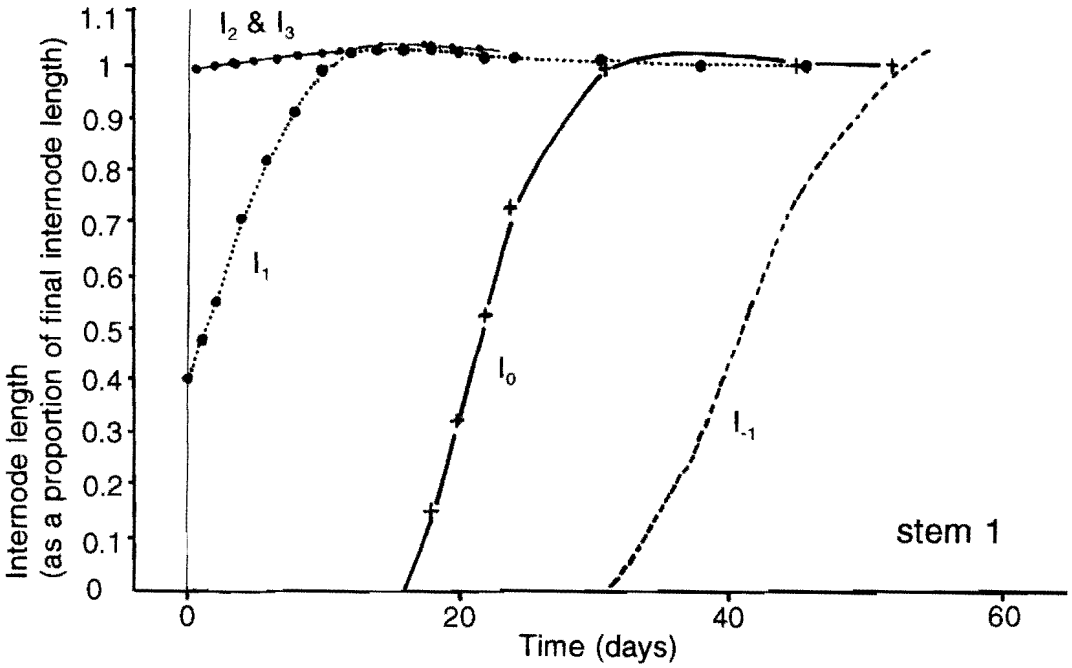

Fig. 2. Changes in internode length (proportion of final length) in the apical region of a *Calamus caesius* stem over 60 days. Internode I_1 (see Fig. 1) was partly expanded at the start of measurements, whilst I_2 and I_3 were already fully expanded. Internodes produced later had an average plastochrone of 20 days.

which (stem 9) is shown (Fig. 4). The mature length of the cirrus is first reached when the leaf (L_0) is one internode above the youngest exposed leaf sheath, while that of the "leaf proper", and the sheath, is first reached at the same time as the leaf sheath is exposed (L_1). This basipetal pattern of development of the leaf was also observed in the other shoot (stem 8) sampled. Expansion of the pinnae occurs and is completed in the leaf with the youngest exposed sheath (L_1). The youngest mature internode (I_1) is that below the youngest mature leaf sheath. This shows that the indirect method for measurement of internode length, by measuring the distance between adjacent knees, is reliable even for the internode (I_1) whose distal end bears the youngest exposed sheath. Thus internode I_1 elongates and pushes the leaf at its distal end, L_1, which reaches its mature length earlier, and the younger internodes, together with the young fronds above them, up the shoot.

The total number of exposed living fronds, defined here as those with exposed pinnae, is 72 and 44 for stems 8 and 9, respectively, whereas that of unexposed fronds is 11 (L_0-L_{-10}) for both stems. An examination of 50 stems in a 13-year-old *C. caesius* plot at Kolapis, 65 km west of Sandakan, gives an average of 63 exposed living fronds (95%

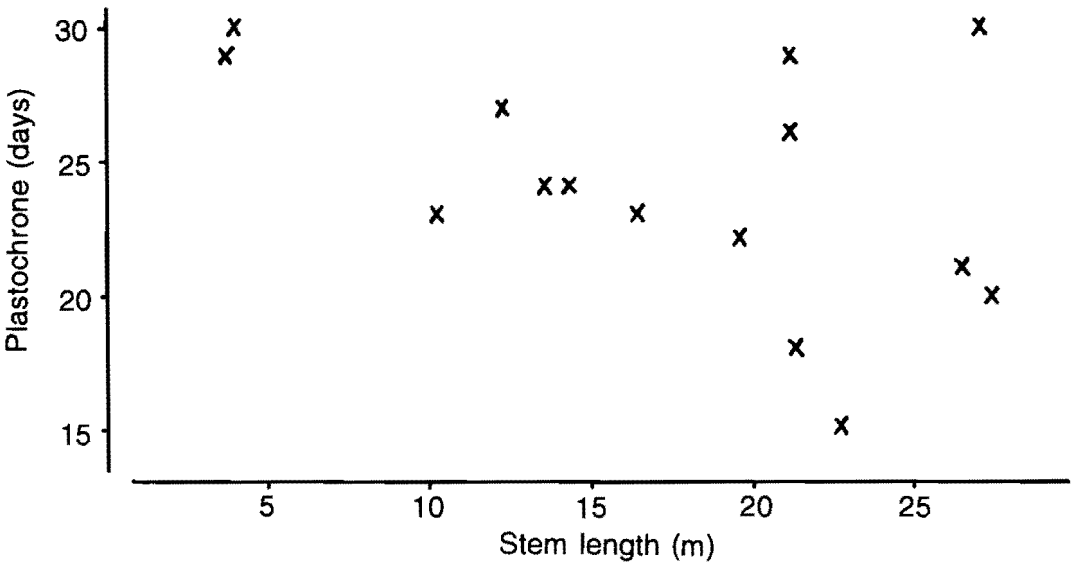

Fig. 3. The time between production of successive internodes (plastochrone, days) plotted against total stem length (m). The apparent correlation is not significant.

confidence interval: 58-67 fronds). Using the mean plastochrone of 24 days, this gives an estimated leaf life span of 1512 days (4.1 years). If the unexposed leaves (counting from the youngest visible primordium) are included, the average number of living leaves is 74, and the equivalent leaf life span is then 1776 days (4.9 years). The ratio of the number of unexposed leaves (including the spear leaves with unexpanded pinnae) to that of exposed leaves was found to be 0.17.

The apical dome, which includes the apical meristem, is defined here as the internodes shorter than 2 mm together with the leaves attached to their distal ends (Fig. 1). The domes of stems 8 and 9 were found to be 78 and 83 cm, respectively, below the distal end of the last exposed leaf sheath (L_1). A similar study on 50 stems in the plot at Kolapis gives an average value of 79 cm (95% confidence interval: 74-84 cm).

Discussion

The plastochrone of 24 days as determined for *C. caesius* in this study gives a growth rate of 15.2 internodes per stem per year. Assuming the average internode length to be

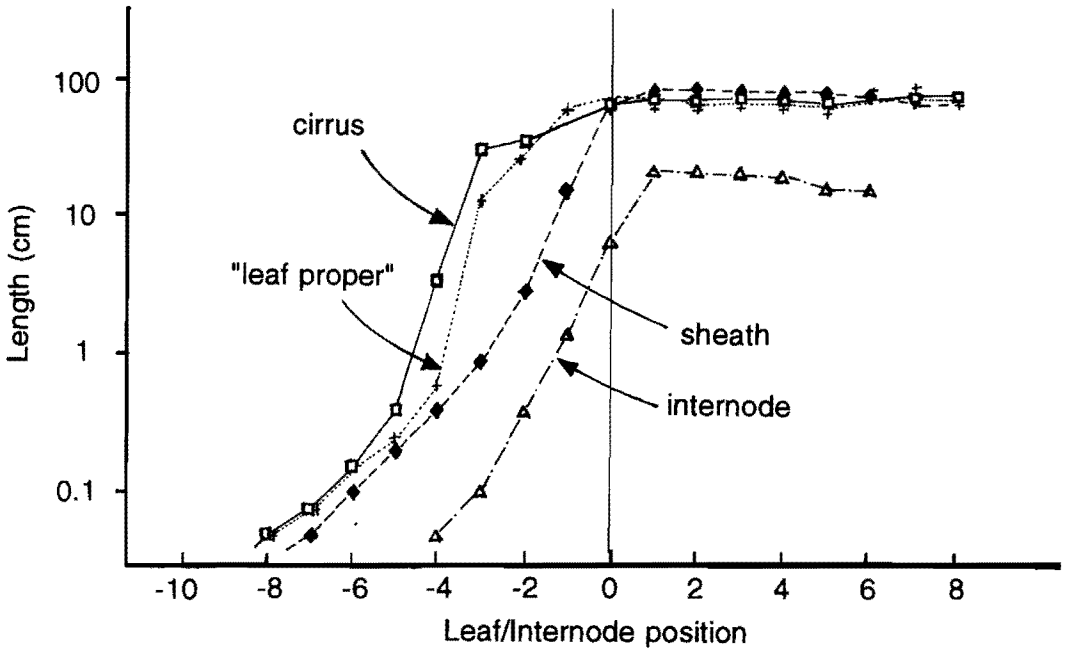

Fig. 4. Growth (cm, log scale) of cirrus, "leaf proper", sheath, and internode in relation to position on the stem (see Fig. 1), in the apical region of a *Calamus caesius* stem.

30 cm, which is the value obtained in this study, the stem growth rate is estimated to be 4.6 m/year. This rate is comparable to the figure of 4 m/year reported by Priasukmana (1986) for the same species but is lower than the 5 m/year and 7m/year reported by Priasukmana (*op.cit.*) and Shim (1989), respectively, for *C. trachycoleus.*

The result of this study shows that the internode (I_1) with the youngest exposed leaf sheath is immature and is, on average, 16% shorter than the fully expanded ones below. Thus, in the application of the yield models which assume constant or gradually increasing internode length from the stem base to tip, it is necessary to deduct 16% of the average internode length for the internode with the youngest exposed sheath in each stem. This study also shows that in the measurement of stem length of *C. caesius,* to determine the actual length of the stem from the base to the apical meristem, about 79 cm should be deducted from the "stem length" normally measured, *i.e.* the distance from the stem base to the distal end of the youngest exposed sheath or last visible knee (marked with an asterisk in Fig. 1).

This leaf sheath (L_1) thus encloses several younger leaves, as also shown by Fisher (1978) for other rattan species, and may protect the apical meristem against herbivores

and pathogens. This can at least partly explain why the apical meristem is seldom damaged in *C. caesius,* as in other rattan species. Protection of the apical meristem is very important in many monocots including rattans because the stem dies if its apex is destroyed.

The number of internodes (11) enclosed by the youngest exposed leaf sheath in *C. caesius* is smaller than that in the large-diameter rattans, *C. manan* and *Daemonorops angustifolia,* which have 15 and 19 internodes, respectively, but is about the same as that in *C. insignis* (Fisher 1978). It can thus be concluded that the apical dome of the small-diameter stem can accommodate fewer internodes than that of the large-diameter ones. The ratio of the number of unexposed leaves (including the spear leaves with unexpanded pinnae) to that of the exposed leaves (0.17), is much lower than the ratio of 1 reported for many palms (Corner 1966, Tomlinson 1990).

The life span (4.9 years) of the leaves of *C. caesius* estimated in this study is comparable to that of such palms as *Cocos nucifera* (5 years; Venkatanarayana 1957) and *Nypa fruticans* (5.5 years; Fong 1986), but is longer than that of other palms, *e.g. Pigafetta filaris* (1.0-1.2 years; Davis & Kuswara 1987) and *Elaeis guineensis* (3.5 years; Rees 1964). There is a large number of old and possibly slowly senescing fronds on *C. caesius* which may have a negative net assimilation rate and could therefore be a burden to the stem. This hypothesis can easily be tested with a suitable experiment such as a frond-pruning trial.

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